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Published in:
Animal Behaviour

DOI:
10.1016/0003-3472(95)80202-9

Publication date:
1995

Anim. Behav., 1995, **49**, 695–708

Transfer experiments of Seychelles warblers to new islands: changes in dispersal and helping behaviour

JAN KOMDEUR*†, ALEXANDRA HUFFSTADT‡, WILLEMIJN PRAST‡, GILL CASTLE§, ROB MILETO§ & JAN WATTEL‡

**Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, U.K.*

and

**National Environmental Research Institute, Department of Wildlife Ecology, Kalø, Grenavej 12, DK-8410 Rønde, Denmark*

‡Zoological Museum, University of Amsterdam, P.O. Box 94766, 1009 AT Amsterdam, The Netherlands

§11 Peace Cottages, Old Coleham, Shrewsbury, Shrops SY5 7BT, U.K.

(Received 20 December 1993; initial acceptance 23 February 1994; final acceptance 30 March 1994; MS. number: 4548)

Abstract. Young of the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis*, frequently remain on their natal territories and act as helpers. Independent reproduction may be constrained by habitat saturation (a shortage of breeding territories) or, alternatively, individuals on good territories may achieve higher fitness by staying and helping than by dispersing and breeding on inferior territories. Transfers of warblers to unoccupied islands showed that both habitat saturation and variation in territory quality dramatically affected the frequency of delayed dispersal. At first there was no cooperative breeding, but as all high-quality areas became occupied, young birds hatched on them began to stay as helpers, rather than occupy breeding vacancies on lower quality territories. However, as the number of helpers on high-quality territories increased, thereby reducing the helper's indirect component of inclusive fitness benefits from staying at home, it paid some helpers to leave, even to poor territories. Thereafter, young reared on poor territories did better to leave to breed on poor territories, rather than stay at home.

Most species of cooperatively breeding birds and mammals exhibit delayed dispersal. Instead of leaving home shortly after reaching independence, mature offspring frequently remain on their natal territories for months or years, assisting their parents in the rearing of young. Despite the large and growing literature on cooperative breeding (Brown 1987; Stacey & Koenig 1990; Emlen 1991; Koenig et al. 1992), it has proved remarkably difficult to reach a consensus on the causes of delayed dispersal. The usual approach is to focus on the 'ecological constraints' (Emlen 1982) that prevent offspring from dispersing early in life and breeding independently. One such constraint is 'habitat saturation': young are constrained from becoming independent breeders by a shortage of breeding territories or mates (Selander 1964; Emlen 1982, 1991; Brown 1987; Koenig et al. 1992). Recently, however, the lifetime inclusive fitness benefits from staying at home have been emphasized (Stacey & Ligon 1987, 1991; Zack 1990). Advocates of this 'benefits of philopatry' viewpoint have proposed that when resources within territories vary in quality, individuals on good territories may achieve higher fitness by staying and helping than by dispersing and breeding on inferior territories.

The relative merits of these two perspectives have been the subject of a lively debate (Stacey & Ligon 1987, 1991; Heinsohn et al. 1990; Zack 1990; Emlen 1991; Koenig et al. 1992; Walters et al. 1992; Brown 1993; Komdeur 1993), but are they really different hypotheses? In this paper we describe two removal experiments of Seychelles warblers, *Acrocephalus sechellensis*, which address both perspectives.

†Present address: Biological Centre, University of Groningen, P.O. Box 14, 9750 AA Haren, The Netherlands.

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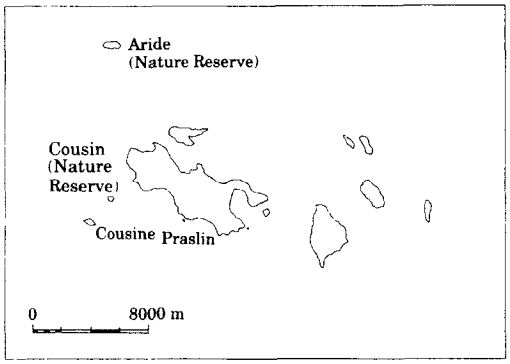

Figure 1. Map showing the Seychelles islands with populations of Seychelles warblers: Cousin, Aride as place of first transfer (23–29 September 1988), and Cousine as place of second transfer (29 June–1 July 1990).

STUDY SPECIES

The Seychelles warbler is a small (15 g) insectivorous bird, endemic to the Seychelles Islands in the Indian Ocean. In 1959, the total population was reduced to 26 individuals, entirely confined to Cousin Island (29 ha; Crook 1960). However, after the island was purchased for the International Council for Bird Preservation (ICBP, now called BirdLife International) in 1968, and efforts were initiated to restore the native vegetation, the warbler staged a dramatic recovery. By 1982, the Cousin population had grown to nearly 320 birds on 115 breeding territories (Bathe & Bathe 1982). Since then numbers of both birds and territories have fluctuated around that level, suggesting that these values reflect the carrying capacity of the island (Komdeur et al. 1991; Komdeur 1992, 1994a). At the same time, delayed dispersal and cooperative breeding became prevalent on Cousin (Komdeur 1992). Given the vulnerability of one small island in the Indian Ocean and the proven suitability of the islands of Aride (68 ha) and Cousine (26 ha) for the establishment of additional warbler populations (Fig. 1), warblers were translocated to these islands in September 1988 and June 1990, respectively (Komdeur 1994a). Aride, 9 km north of Cousin, is a nature reserve run and owned by the Royal Society for Nature Conservation (RSNC). Cousine is a privately owned, rat-free island in a nearly natural state. Remarkably, even though Cousine is only 1·6 km from Cousin, no warblers reached it prior to their introduction (G. Souffe, personal communication). The total population on the three islands is now well over 500 individuals (Komdeur 1994a).

Observational data suggest that the frequency of delayed dispersal and cooperative breeding on Cousin Island is influenced not only by habitat saturation, but also by territory quality (measured in terms of food availability); 1-year-old warblers (who are adults and can breed successfully) from high-quality territories are much more likely to remain and help on their natal territories than are yearlings from lower quality territories (Komdeur 1992). Delayed dispersal of offspring was not influenced by a shortage of mates, as additional males and females were abundant on Cousin (Komdeur 1991). Removal experiments showed that the presence of one or two helpers on good-quality territories on Cousin Island improved the reproductive success of their parents whereas the presence of three or more helpers apparently had a negative effect on reproductive success (Komdeur 1994b). Several lines of evidence suggest that the latter may have been caused by the reduction in available food when a large number of offspring remained on their natal territory. As the costs of helping are negligible, and helping does not influence breeders' survival, the increased reproductive success of groups with one or two helpers is entirely the result of helping, thereby improving the helper's indirect component of inclusive fitness benefits from staying at home (Komdeur 1994b). Individuals that delay reproduction in high-quality territories, but eventually breed there, have greater lifetime fitness (both survival and reproductive success are higher) than those that disperse at 1 year of age and breed immediately in lower quality territories (Komdeur 1992). With a large range in the quality of available territories, selection should favour individuals that delay dispersal and wait for a high-quality opening rather than accept the first vacancy available. Removal of warblers to the unoccupied island of Aride showed that group living is promoted by competition for high-quality territories, thereby supporting the 'benefits of philopatry' hypothesis for cooperative breeding (Komdeur 1992).

The transfers of Seychelles warblers to the unoccupied islands of Aride and Cousine allowed us to test the 'ecological constraints' model and the 'benefits of philopatry' model for cooperative breeding, independently. If habitat saturation is

responsible, cooperative breeding on the new islands should occur only when carrying capacity is reached. If gains in lifetime inclusive fitness benefits are important, then cooperative breeding is expected to start when high-quality areas are completely covered with territories, but before the breeding population reaches carrying capacity. In this paper we investigate the effects of territory quality, habitat quality and habitat saturation on delayed dispersal and cooperative breeding in the Seychelles warbler, by comparing the reproductive rates, the frequency of delayed dispersal and cooperative breeding on the saturated Cousin Island and on the unsaturated, previously unoccupied islands of Aride and Cousine.

METHODS

Study Area and Study Population

Over 23–29 September 1988, 29 colour-ringed adult Seychelles warblers (16 males and 13 females) were transferred by boat from Cousin Island to Aride. These consisted of 17 experienced birds (which had held a territory and bred at least once), six helpers and six philopatric non-helpers. Six groups were transferred as family groups consisting of the breeding pair and an adult offspring. The pair formation remained the same after the transfer. Over 3 days (29 June–1 July 1990), 29 colour-ringed adult warblers (15 males and 14 females) were transferred from Cousin Island to Cousine Island. These consisted of 16 experienced birds, nine helpers and four non-helpers.

On Cousin and Aride the warblers were studied simultaneously from September 1988 to November 1991, and on Cousine from June 1990 to November 1991, as part of a study of cooperative breeding in the Seychelles warbler. On Cousin all 115–123 groups of the warblers (300–360 birds) were studied from September 1988 to June 1990, and 39 groups (139–151 birds) from June 1990 to June 1991 by J.K., and 35 groups (89–103 birds) from July to November 1991 by A.H. and W.P. On Aride, 13–43 groups (29–180 birds) were studied from September 1988 to November 1991 by J.K., G.C. and R.M. Additional monitoring of the warbler population on Aride was conducted by volunteers and the wardens, and by J.K. during two visits in August 1993 and in July 1994, respectively. On Cousine an additional 12–16 groups (29–43 birds) were studied from June 1990 to June 1991 by J.K., and 10 groups (25–35 birds) from July to November 1991 by A.H. and W.P. The average yearly percentage of birds that were individually colour-ringed was 70% on Cousin, 74% on Aride and 90% on Cousine.

General Methods and Data Collection

On Cousin, Aride and Cousine, as many young as possible were colour-ringed. On Aride and Cousine, twice a month, the island was searched to locate dispersing birds and to plot new territories using a portable tape-recorder with a continuous loop cassette of male song to attract birds. As the three islands have the same habitat types and are very close to each other, we employed matched-pairs statistical tests to compare breeding activity between them.

Breeding Activity and Offspring Dispersal

To record breeding activity, the territories on Cousin, Aride and Cousine were checked fortnightly for active nests by following females for 30 min continuously. This observation period was long enough to determine whether birds were breeding; a breeding female was involved in either nest building, incubating or feeding for at least two 30-s intervals during this period (Komdeur 1991). All nests were checked for clutch size, sometimes with the help of a long stick and angled mirror. Observations on nest building, incubating, and feeding young were made for 3 h. Feeding observations started in the second week after hatching and were repeated every 3 weeks until the young died or reached independence. For each 30 s we noted whether each bird was taking part in each of the above mentioned categories.

At the same time, each territory was checked for the presence of unringed and colour-ringed birds, the latter to determine the proportion of birds that died or survived. Once a bird was missing from its territory, all other territories and vacant areas were checked to assess dispersal. As emigration from the study area never occurred, we assumed that missing birds had died.

Territory Quality

Territory quality could be measured in terms of availability of nest sites, density of predators or

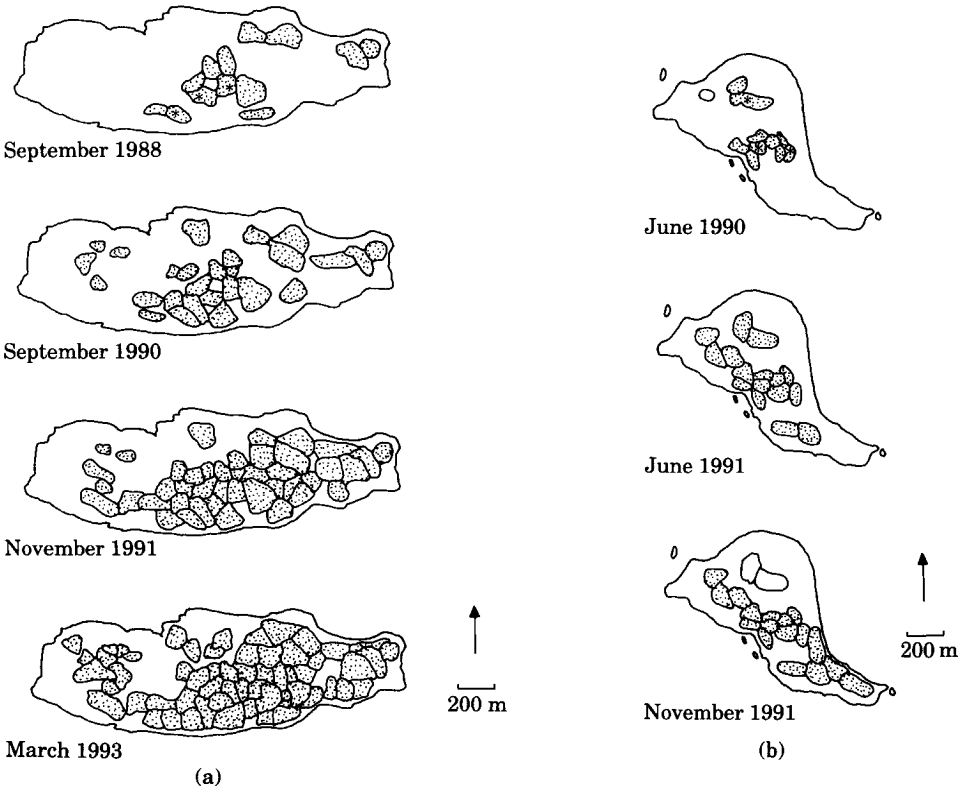

Figure 2. Seychelles warbler territories on Aride Island (a) in September 1988 (at the time of transfer), in September 1990, in November 1991 and in March 1993 (Taylor & Dixon 1993), and on Cousine Island (b) in June 1990 (at the time of transfer), in June 1991 and in November 1991. Release points are indicated by asterisks.

food availability. On the three islands nest sites had no consistent features (within the same territory nests were found from 1 m to as high as 20 m) and were abundant. Adult Seychelles warblers lack natural predators. Nest predators, Seychelles fodies, *Foudia sechellarum*, which are weaver birds endemic to the Seychelles, and two endemic skink species, *Mabuya wrightti* and *M. sechellensis*, were evenly distributed over the islands (Brooke & Houston 1983; Owen 1986; Komdeur 1994a). We therefore measured territory quality in terms of number of arthropod prey available. As the warblers are insectivorous, taking 98% of their insect food from leaves (Komdeur 1991), territory quality (tq) depends on insect prey available and amount of foliage present, which was measured as:

$$tq = a \sum_{x=1}^{12} (c_x i_x) \cdot$$

where a is mean annual territory size (ha), c_x is mean foliage cover for plant species x, and i_x is mean insect totals for plant species x per unit leaf area (1 dm^2) in the territory. The only other insect-eating bird species present on the islands were the Seychelles fody and the endemic Seychelles sunbird, *Nectarinia dussumieri*.

We measured the amount of foliage in each territory using a transect method. The transect through each territory was 250 m long, subdivided into straight subtransects plotted 25 m apart and facing north from one territory boundary to the other. Every 5 m the presence or absence of foliage and the plant species were noted in the following heights: 0·0–0·75 m, 0·76–2·0 m, 2·1–4·0 m, and at 2-m intervals thereafter. Total foliage cover for plant species x (c_x) is the number of cases of presence of foliage at all heights along the transect.

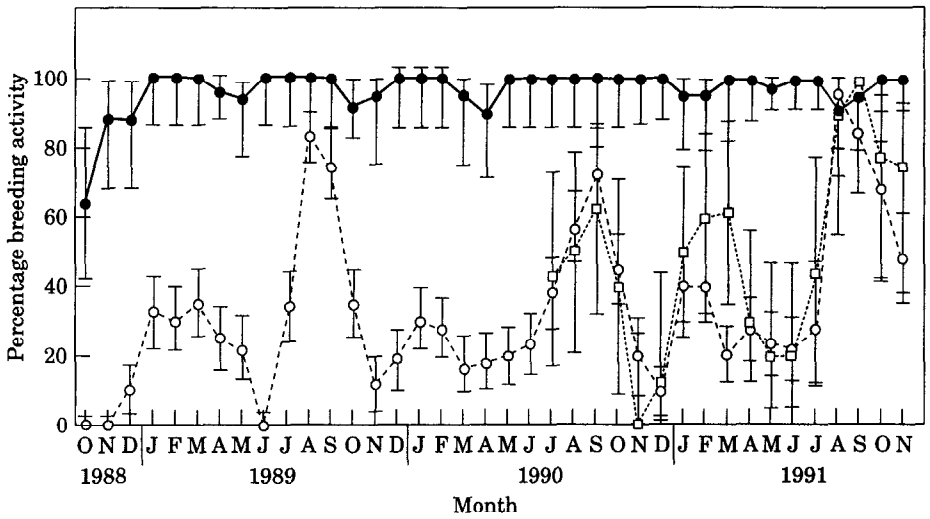

Figure 3. Percentage territories with breeding activity (nest building, incubating, or feeding young) each month (± 95% confidence limits) on the islands of Aride (●), Cousin (○) and Cousine (□). Mean breeding activity Aride and Cousin (October 1988–November 1991): 97% (mean $N=21$) and 34% (mean $N=82$), respectively. Mean breeding activity Aride, Cousin and Cousine (July 1990–November 1991): 98% (mean $N=19$), 44% (mean $N=38$) and 49% (mean $N=12$), respectively.

To assess prey availability (i_x) in each territory, we searched the upper- and under-sides of 50 leaves per plant species (12 dominant species) for insects. To assess insect density for plant species x, the area of 250 leaves for each species was measured at 50 random sites on the island (five leaves per site).

Every 3 months (between 15 and 29 of each month) the quality of all territories under study was assessed simultaneously on Cousin and on Aride from September 1988 to June 1991, and on Cousine from June 1990 to June 1991. At the same time, the quality of 20 randomly distributed unoccupied areas (control areas) on Aride and Cousine was assessed. This was done to find out whether the warblers preferred to colonize habitats of particular quality. The control areas were of the same size and shape as an average territory on that island at that time. In September and November 1991, the quality of 10 territories (out of 25) on Cousin, four territories and two control areas on Cousine was assessed. Territories were divided into three categories: low (tq=0·0–15·0), medium (tq=15·1–30·0) and high quality (tq=30·1–45·0). High-quality areas on the new islands were scored as 'completely occupied' by territories, when the highest quality value of one of the control areas was significantly less than the average quality of the occupied high-quality territories.

RESULTS

Breeding Activity following Transfers

The transferred birds on Aride and Cousine formed pairs with their original or new mates and began establishing territories within days, and in some cases hours, of being released (Fig. 2). At the beginning of October 1988, 13 territories were established on Aride; 11 were occupied by pairs and two by single males. The other five birds were seen wandering all over the island on their own. At the beginning of July 1990, 12 territories were established on Cousine; eight were occupied by pairs and four by single males. The other nine birds were seen wandering over the island on their own. The most striking aspect of both transfers was the burst of nesting activity by birds immediately following release, and that breeding on Aride occurred outside the 'normal' breeding period. On both islands, successful nesting started in most territories within a few weeks, and in some territories within 3 days, of release. The first

Table I. Comparison of annual adult survival, breeding performance (± SD) of Seychelles warblers and territory quality on the islands of Aride and Cousin during the first (October 1988–September 1989), the second (October 1989–September 1990) and the third year (October 1990–September 1991) following the transfer

	Aride	Cousin	*P*
October 1988–September 1989			
N	11	49	
Annual adult survival	100 (29)	80·3 (117)	<0·025
Nest-building attempts			
Per territory	5·55 ± 1·55	1·93 ± 1·06	<0·001
Total	61	95	
Nests with clutches (%)	88·5	64·2	<0·005
Number of nests with clutches			
Per territory	4·91 ± 1·17	1·24 ± 0·99	<0·001
Total	54	61	
Mean clutch size	1·85 ± 0·52 (20)	1·00 ± 0·00 (55)	<0·005
Clutches hatched (%)	70·4	69·7	NS
Number of nests with pulli			
Per territory	3·46 ± 1·08	0·76 ± 0·82	<0·001
Total	38	37	
Mean no. of days to fledge	14·0 ± 0·87 (26)	18·8 ± 1·35 (22)	<0·001
Nestlings fledged (%)	76·3	83·8	NS
Number of nests producing fledglings			
Per territory	2·64 ± 0·80	0·63 ± 0·71	<0·001
Total	29	31	
Fledglings reaching 1 year of age (%)	100·0	29·0	<0·001
Number of yearlings produced			
Per territory	2·64 ± 0·80	0·19 ± 0·17	<0·001
Total	29	9	
Mean territory quality	327 ± 31·2 (11)	15·5 ± 10·3 (49)	<0·001
October 1988–September 1990			
N	18	49	
Annual adult survival	100 (36)	83·3 (132)	<0·025
Nest-building attempts			
Per territory	5·22 ± 1·49	1·67 ± 0·99	<0·001
Total	94	82	
Nests with clutches (%)	87·2	58·5	<0·001
Number of nests with clutches			
Per territory	4·56 ± 1·04	0·98 ± 0·75	<0·001
Total	82	48	
Mean clutch size	1·75 ± 0·40 (24)	1·00 ± 0·00 (48)	<0·005
Clutches hatched (%)	67·1	64·6	NS
Number of nests with pulli			
Per territory	3·17 ± 0·95	0·63 ± 0·69	<0·001
Total	57	31	
Mean no. of days to fledge	14·1 ± 0·77 (29)	19·1 ± 1·15 (22)	<0·001
Nestlings fledged (%)	78·9	77·4	NS
Number of nests producing fledglings			
Per territory	2·50 ± 0·84	0·49 ± 0·58	<0·001
Total	45	24	
Fledglings reaching 1 year of age (%)	100·0	33·3	<0·001
Number of yearlings produced			
Per territory	2·50 ± 0·84	0·16 ± 0·16	<0·001
Total	45	8	
Mean territory quality	288 ± 32·2 (18)	17·3 ± 14·2 (49)	<0·001

Table I. *Continued*

	Aride	Cousin	*P*
October 1990–September 1991			
N	15	35	
Annual adult survival	96·7 (30)	78·8 (85)	<0·05
Nest-building attempts			
Per territory	5·27 ± 1·20	2·11 ± 0·81	<0·001
Total	79	74	
Nests with clutches (%)	73·4	59·5	<0·025
Number of nests with clutches			
Per territory	3·87 ± 1·35	1·26 ± 0·41	<0·001
Total	58	44	
Mean clutch size	1·25 ± 0·43 (20)	1·11 ± 0·33 (9)	NS
Clutches hatched (%)	75·9	72·7	NS
Number of nests with pulli			
Per territory	2·93 ± 1·31	0·91 ± 0·40	<0·001
Total	44	32	
Mean no. of days to fledge	15·1 ± 0·70 (10)	19·0 ± 0·58 (6)	<0·001
Nestlings fledged (%)	90·9	84·4	NS
Number of nests producing fledglings			
Per territory	2·67 ± 1·04	0·77 ± 0·46	<0·001
Total	40	27	
Fledglings reaching 1 year of age (%)	100·0	44·4	<0·025
Number of yearlings produced			
Per territory	2·67 ± 1·04	0·34 ± 0·24	<0·001
Total	40	12	
Mean territory quality	213 ± 38·2 (15)	19·4 ± 15·2 (10)	<0·001

Figures in parentheses are number of observations (or number of bird-years for survival data).
N=Number of observed territories. Statistical significance of comparisons determined by chi-squared contingency analysis (percentage data) or two-tailed *t*-test.

young on Aride (twins) and Cousine were hatched by experienced breeders, 4 and 3 weeks after the transfer, respectively (Komdeur 1994a).

Comparing breeding activity on Aride and Cousin for the 3 years and 2 months after the transfer (Fig. 3), Aride birds showed on average 2·9 times more breeding activity than Cousin birds (paired-sample *t*-test: $t=10{\cdot}36$, $df=37$, $P<0{\cdot}001$). The seasonal pattern in the percentage of territories with breeding activity on Aride was not correlated with that on Cousin in the same month (Spearman rank correlation: $r_S=0{\cdot}19$, $N=38$, $P=0{\cdot}242$). A minimum of 64% of pairs bred on Aride in October 1988 and a maximum of 90–100% of pairs were breeding from January 1989 to November 1991. Over the same period the percentage of breeding pairs on Cousin varied from 0% (October and November 1988 and June 1989) to 96% (August 1991 only). Comparing breeding activity on the three islands for 1 year and 5 months following the transfer to Cousine (Fig. 3), Cousine birds showed the same breeding activity as Cousin birds ($t=1{\cdot}50$, $df=16$, $P=0{\cdot}153$), but 2·0 times less than Aride birds ($t=8{\cdot}53$, $df=16$, $P<0{\cdot}001$). There appeared to be two annual peaks of breeding activity in the populations on Cousin and Cousine; one in August–October and another in January–March. The seasonal pattern in the percentage of territories with breeding activity on Cousine was synchronous with that on Cousin in the same month ($r_S=0{\cdot}83$, $N=17$, $P=0{\cdot}001$).

In each year over the 3 years (October 1988–September 1989; October 1989–September 1990; October 1990–September 1991) following the transfer to Aride, the production of offspring per territory on this island was significantly higher than that of Cousin (Table I). The increase in reproduction can be attributed to three factors: (1) more nesting attempts per territory (on average 2·8 times as many); (2) higher percentage of nests in which a clutch was laid (1·4 ×), and

consequently more nests with clutches per territory (4·6 ×); and (3) higher survival of fledglings to 1 year of age (2·8 ×), and consequently more 1-year-old young produced per territory. In addition young fledged 4–5 days earlier and during the 2 years following the transfer mean clutch size was almost twice as high. Hatching and fledging success were not significantly higher on Aride. Taken together, the production of yearlings per territory was on average 11·3 times higher on Aride. Annual adult survival (the probability of surviving to the next year, starting at age of 1 year) was also significantly higher on Aride (Table I). Given that mean territory quality on Aride was 15·9 times higher than that on Cousin during the 3 years (Table I), it is no wonder that Aride birds were able to sustain high breeding output. In September 1991, 3 years after the transfer to Aride, all 29 transferred birds were still alive and 151 young had fledged successfully (Lidstone-Scott 1993; Komdeur 1994a).

Despite the same breeding activity by warblers on Cousine and Cousin (Fig. 3), the production of offspring per territory on Cousine in the first year (July–November 1990) following the transfer was significantly higher than that on Cousin (Table II), mainly because more nests were built per territory (2·4 times as many). The percentage of nests with clutches, clutch size, hatching success, mean number of days nestlings spent in the nest, and fledging success were all slightly, but not significantly, higher on Cousine. In addition, fledgling survival to 1 year of age was more than twice as high on Cousine. Taken together, these factors resulted in a five times higher production of yearlings. Adult survival was also significantly higher on Cousine (Table II). Mean territory quality on Cousine was 3·4 times higher than that on Cousin (Table II). In June 1991, 1 year after the transfer to Cousine, all transferred birds were still alive and 14 young had fledged successfully (Komdeur 1994a).

During the same period in the second year (July–November 1991), adult birds survived significantly better, but the reproductive output per warbler territory on Cousine was similar to that on Cousin (Table II). The number of nest-building attempts per territory, and the number of nests resulting in clutches, pulli and fledglings were the same. Moreover, on both islands hatching success and survival of nestlings to fledging were the same. These results are in agreement with the fact that the quality of territories on Cousine for warblers had declined (Table II). With an expanding population more territories were established within the high-quality areas leading first to complete occupation of this area, and second to smaller, and thus lower quality territories. As a consequence, birds spread into poorer habitats (see below).

Dispersal of Juveniles

During the 3 years and 2 months following the transfer to Aride and the 1·5 years following the transfer to Cousine, there was still enough space left on Aride and Cousine for young birds to establish new territories (Fig. 2). At first, during the 2 years following the transfer to Aride and the first year following the transfer to Cousine, all the offspring initially produced by translocated birds left their natal territories significantly earlier than young on Cousin (Table III). Juveniles left their natal territories on Aride and Cousine 8 weeks after reaching independence, on average 5·8 times earlier than on Cousin Island. Cousin juveniles from the highest quality territories stayed in their natal territories for on average 43·2 months ($N=20$). On Aride and Cousine, between the time of leaving and pair formation, young birds were seen wandering all over the island. They all paired and established territories of their own within 1 year, and bred significantly earlier than those on Cousin (Table III). None of the 105 birds that was old enough to be a helper (91 and 14, respectively) acted as a helper on their natal territories, and all were able to establish breeding territories of similar quality to their natal territories (mean quality of breeding versus natal territory ($\pm$ SD) on Aride: $287 \pm 39{\cdot}4$ versus $281 \pm 37{\cdot}3$; paired-sample t-test: $t=0{\cdot}43$, $df=90$, $P=0{\cdot}589$; on Cousine: $47{\cdot}9 \pm 6{\cdot}2$ versus $47{\cdot}6 \pm 7{\cdot}7$; paired-sample t-test: $t=0{\cdot}69$, $df=13$, $P=0{\cdot}50$).

Cooperative Breeding

By September 1990, 2 years after the transfer to Aride, and by September 1991, a little more than 1 year after the transfer to Cousine, the highest quality of one of the control areas on these islands became significantly less than the mean quality of all occupied territories (Fig. 4), suggesting that the best-quality habitats on both islands had become occupied. This remained so until the end of the

Table II. Comparison of annual adult survival, breeding performance (± SD) of Seychelles warblers and territory quality on the islands of Cousine and Cousin during the first 5 months in the first year (July–November 1990) and the first 5 months in the second year (July–November 1991) following the transfer

	Cousine	Cousin	*P*
July–November 1990			
N	10	39	
Annual adult survival	100 (29)	81·3 (75)	<0·05
Nest-building attempts			
Per territory	2·00 ± 0·67	0·85 ± 0·56	<0·001
Total	20	33	
Nests with clutches (%)	85·0	78·8	NS
Number of nests with clutches			
Per territory	1·70 ± 0·71	0·67 ± 0·31	<0·001
Total	17	26	
Mean clutch size	1·13 ± 0·33 (8)	1·09 ± 0·29 (22)	NS
Clutches hatched (%)	47·1	46·2	NS
Number of nests with pulli			
Per territory	0·80 ± 0·51	0·31 ± 0·27	<0·001
Total	8	12	
Mean no. of days to fledge	18·8 ± 0·43 (4)	19·0 ± 1·35 (12)	NS
Nestlings fledged (%)	87·5	83·3	NS
Number of nests producing fledglings			
Per territory	0·70 ± 0·46	0·26 ± 0·25	<0·001
Total	7	10	
Fledglings reaching 1 year of age (%)	85·7	40·0	<0·05
Number of yearlings produced			
Per territory	0·60 ± 0·44	0·12 ± 0·21	<0·001
Total	6	4	
Mean territory quality	53·2 ± 5·2 (10)	15·6 ± 10·3 (39)	<0·001
July–November 1991			
N	10	35	
Annual adult survival	100 (26)	80·3 (80)	<0·05
Nest-building attempts			
Per territory	1·10 ± 0·30	1·17 ± 0·45	NS
Total	11	41	
Nests with clutches (%)	90·1	85·4	NS
Number of nests with clutches			
Per territory	1·00 ± 0·45	1·00 ± 0·48	<0·0
Total	10	35	
Clutches hatched (%)	90·0	74·3	NS
Number of nests with pulli			
Per territory	0·90 ± 0·30	0·74 ± 0·44	NS
Total	9	26	
Nestlings fledged (%)	100	84·6	NS
Number of nests producing fledglings			
Per territory	0·90 ± 0·30	0·63 ± 0·48	NS
Total	9	22	
Mean territory quality	41·6 ± 8·9 (4)	20·9 ± 19·2 (10)	NS

Figures in parentheses are number of observations (or number of bird-years for survival data).

N=Number of observed territories. Annual adult survival=$(b/a)^{12/N}$, where a is the number of ringed birds present early July, b is the number of ringed birds still present late November and N=5; the number of months between counts in July and November. Statistical significance of comparisons determined by chi-squared contingency analysis (percentage data) or two-tailed t-test.

Table III. Age of dispersal and first breeding, and percentage of territories with helpers on the saturated Cousin Island (1986–1991) and the unsaturated islands of Aride (October 1988–September 1990) and Cousine (June 1990–June 1991)

				*P**	
	Aride	Cousine	Cousin	Aride–Cousin	Cousine–Cousin
Age young disperse (months)	4·0 ± 0·7 (N=85)	4·2 ± 0·9 (N=14)	23·3 ± 16·4 (N=93)	<0·001	<0·001
Age first breeding (months)	8·1 ± 0·9 (N=61)	8·3 ± 0·8 (N=4)	47·3 ± 15·8 (N=44)	<0·001	<0·001
Territories with helpers (%)	0·0 (y=2)	0·0 (y=1)	25·5 (y=6)	<0·001†	<0·001†

N=Number of individuals; y=number of years.
*t-test comparing the unsaturated island and Cousin Island.
†t-test was calculated using arcsine transformations.

observation period (November 1991). Another source of evidence of habitat saturation within high-quality areas was the temporal occupation pattern of areas of different quality. With a range of habitat qualities available, we predicted that the best should be occupied first (highest fitness output), with overflow into poorer habitats once the best habitat was saturated. On Aride Island, only high-quality territories were occupied until June 1990 (Fig. 5a). Thereafter, the number of high-quality territories remained rather constant,

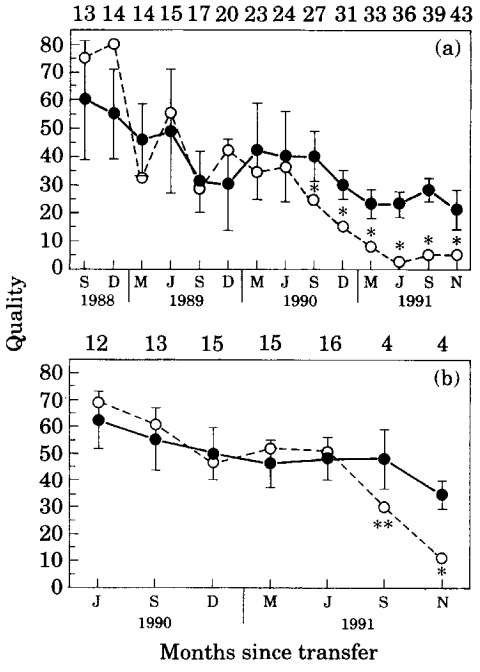

Figure 4. Mean territory quality (●) and highest quality value of unoccupied areas (○) on the islands of Aride (a) and Cousine (b) (top figures are number of territories; number of unoccupied areas is 20 for all periods, except for September and November 1991 where N=2 for Cousine Island). Statistical significance of comparisons determined by one-tailed t-test. *P<0·0025; **P<0·025.

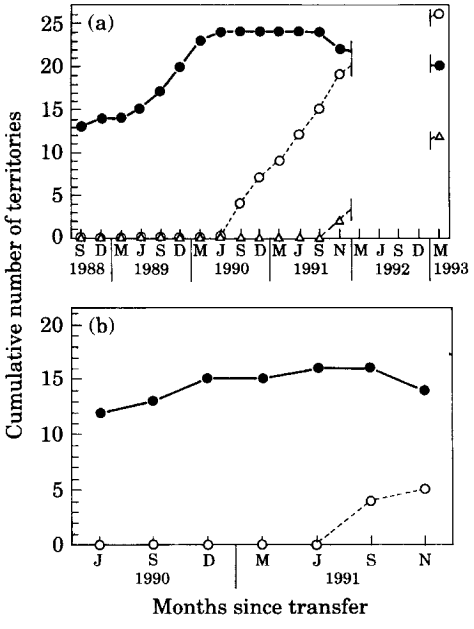

Figure 5. Effect of territory quality on dispersal by Seychelles warblers on the islands of Aride (a) and Cousine (b). ●: High-quality territory; ○: medium-quality territory; △: low-quality territory.

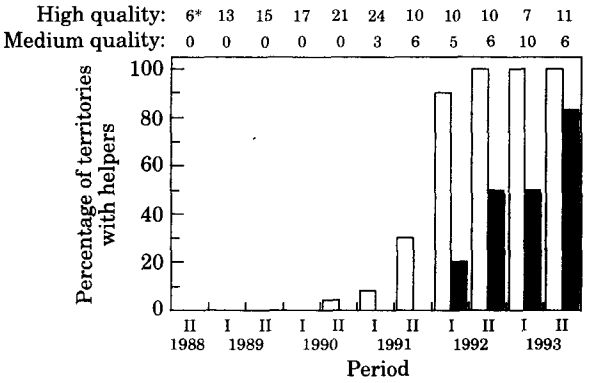

Figure 6. Percentage of high- (□) and medium-quality (■) territories with helpers on the unsaturated Aride Island (I: January–June; II: July–December; 1988–1993). Top figures are numbers of territories, which could have had helpers, because potential helpers and nests with young were present (*potential helpers from six territories on Cousin Island, which were transferred to Aride Island with their parents).

and so the high-quality habitat seemed to be saturated. Territories were subsequently established in medium-quality habitat until September 1991, and in low-quality habitat from November 1991 onwards (Fig. 5a). From November 1991, the number of high-quality territories declined because they disintegrated resulting in more medium-quality territories within the high-quality area. In November 1991 a new breeding pair defended and budded off part of two territories in the high-quality area. Subsequently a new territory was formed, at the expense of the other two territories, resulting in three medium-quality territories within the high-quality area. In March 1993 two high-quality territories had been transformed into six medium-quality territories (Taylor & Dixon 1993; Fig. 5a). On Cousine Island, only high-quality territories were established until June 1991 (Fig. 5b). Thereafter, with the high-quality area being fully occupied, new territories were established in the medium-quality habitat and in the high-quality habitat by taking over part of the existing territories. In November 1991 two breeding pairs established territories in the high-quality area at the cost of two existing territories, resulting in four medium-quality territories (Fig. 5b).

In October 1990, 2 years after the transfer, three 1-year-old birds on Aride hatched on high-quality territories stayed on their natal territories as helpers, even though there was still abundant space for them in lower quality areas to establish territories (Fig. 2). Since then, helping on high-quality territories on Aride has become more and more common, and since 1992 it has been observed in all high-quality territories (Fig. 6). In August 1993, the largest group size recorded was 17 birds in a high-quality territory. The group contained three breeding pairs, helpers and non-helpers, all family members but of variable relatedness. In January 1992, helping on medium-quality territories was observed, and has since become a common phenomenon (R. Lidstone-Scott, unpublished data), even though there is enough space for new territories in low-quality territories (Fig. 2). So far, no helpers have been observed in low-quality territories. In September 1991, 1 year and 4 months after the transfer, the first helper on Cousine was observed. This was a 13-month-old bird, hatched on a high-quality territory, which helped its parents defend the nest and territory, and feeding twins, both in the nest and while fledged. Since the first observations of helping activity, other young hatched on high-quality territories have begun to stay as helpers on Cousine (J. Neville, personal communication), while there is still abundant space for them to establish territories in lower quality areas (Fig. 2; J. Neville, personal communication).

DISCUSSION

Effect of Territory Quality on Reproduction and Survival

Even on a small island like Cousin, the quality of territories (measured as insect prey available)

varied significantly. Territory quality was significantly associated with foraging efficiency of warblers; birds on high-quality territories not only spent less time foraging but also had higher foraging success (mean number of pecks after which the bird was seen swallowing food per 30 s) and caught more energy-rich prey than birds on lower quality territories (Komdeur 1991). An increase in foraging efficiency presumably affects the amount of energy that can be allocated to reproduction without incurring additional survival costs. Overall, the number of young fledged and survival of both juveniles and adults were significantly related to territory quality (Komdeur 1991). Because gross differences in territory quality cause variation in reproduction and survival, they also significantly affect the fitness of a bird, measured in terms of the number of young produced in a lifetime.

During the 3 years after the transfer to Aride and the first year after the transfer to Cousine, mean territory quality on these islands was significantly higher than that on Cousin, leading to higher reproductive success per territory and survival of juveniles and adult birds. Another cause of higher adult survival could be age-specific survival rates; annual survival on Cousin Island improved up to age 6 and deteriorated after age 7 (Komdeur 1991). The current population on Aride may have higher annual survival rates because it is young; all the warblers, except those survivors of the 29 founder birds, are under 5·5 years old. All young birds were able to establish high-quality territories and to breed within their first year of life. During the second year, however, more territories were established within the high-quality area, leading to habitat saturation within this area, and smaller territories (and hence, to declining territory quality) at a later stage. Thereafter, new territories began to be established in the unsaturated medium-quality habitat. As a consequence, mean territory quality on Cousine declined and ultimately approached the levels found on Cousin territories. As a consequence, reproductive output per territory and survival of birds on Cousine declined to become the same as those on Cousin. On Aride, during the third year after the transfer, mean territory quality was still higher than that on Cousin, and in the fourth year, new territories began to be established in the low-quality habitat, because of saturation of the medium-quality habitat. However, once all areas have been filled and territories have become smaller and declined in quality, we expect that reproductive output per territory and survival of birds on Aride will be the same as on Cousin.

Habitat Saturation and Territory Quality

The transfers of warblers to the unoccupied islands of Aride and Cousine were the strictest experimental tests of the 'benefits of philopatry' hypothesis for cooperative breeding. Initially, on the unsaturated islands Aride (until October 1990) and Cousine (until September 1991), all young birds (91 and 14, respectively) were able to establish new territories and find mates, and split off from the natal groups immediately after independence. The offspring sex ratio on both islands was not biased towards a particular sex (sex ratio Aride (female:male): 1·01:0·99, $N=79$; sex ratio Cousine: 1:1, $N=6$). Thus, in the absence of habitat saturation and shortage of mates, delayed dispersal and cooperative breeding simply did not occur. Only later, more than 2 years after the transfer to Aride and more than 1 year after the transfer to Cousine, when all of the high-quality areas became occupied, did young birds hatched on high-quality territories begin to remain on their natal territories and act as helpers, rather than occupy breeding vacancies on lower quality territories. However, as the number of helpers on high-quality territories increased, thereby reducing the helper's indirect component of inclusive fitness benefits from staying at home (Komdeur 1994b), it paid some helpers to leave, even to lower quality territories where direct benefits from breeding independently were greater (Komdeur 1994b). Three and a half years after the transfer to Aride, all of the medium-quality sites became filled, and helping on medium-quality territories started, even though there was still space on low-quality areas for the establishment of territories. Young reared on low-quality territories did better to leave to breed on poor territories, rather than stay at home (Komdeur 1994b). These results were not biased by a shortage of mates, as offspring sex ratio at the time of cooperative breeding was equal males and females (sex ratio Aride 1·08:0·92, $N=50$; sex ratio Cousine 0·8:1·2, $N=9$).

Presented with these unequivocal experimental results, it is clear that the combination of

habitat saturation and variation in territory quality has a profound effect on the expression of delayed dispersal and cooperative breeding in the Seychelles warbler. One cannot simply talk about 'habitat saturation' being the cause of delayed dispersal and cooperative breeding: it is necessary to consider saturation of habitats of different quality because a young bird's decision whether to stay or disperse depends on the relative quality of its natal territory compared with potential breeding territories. These influence the payoffs from staying versus breeding. In other words, dispersal decisions are influenced not only by quality of breeding vacancies, but also by quality of natal territory. Different birds may 'see' different levels of habitat saturation, depending on the quality of their natal territory.

Evolution of Cooperative Breeding

As dispersal decisions in cooperatively breeding birds are influenced by a variety of ecological factors (Emlen 1982; 1991; Brown 1987; Stacey & Ligon 1987, 1991; Zack & Rabenold 1989; Pruett-Jones & Lewis 1990; Zack 1990; Koenig et al. 1992; Walters et al. 1992), it was originally thought that delayed dispersal was a problem with far too many solutions. For this reason, it may be more productive to focus on the causes of variation in its expression, rather than on the causes of delayed dispersal itself.

Our study demonstrates clearly that the causes of variation in dispersal tendencies at one level may not account for variation at other levels; the primary cause of within-population variation in delayed dispersal is variation in territory quality, but the primary cause of between-population variation in delayed dispersal is the degree of habitat saturation. Similarly, if we were to take a comparative perspective and ask why the Seychelles warbler exhibits delayed dispersal and cooperative breeding, but other species of *Acrocephalus* do not, we may get an answer that has nothing to do with either habitat saturation or variation in territory quality. That is, a hypothetical closest relative of the Seychelles warbler may live in environments that are just as saturated and just as variable in quality as Cousin Island, but none the less may breed non-cooperatively, because of other more important ecological factors.

ACKNOWLEDGMENTS

We thank Nick Davies (Cambridge University, U.K.) for his extremely constructive feedback during this study. We are also grateful to Michael Rands (BirdLife International, U.K.), who arranged permission for the transfer, to Christopher Cadbury and Robert Vogel who generously provided support and agreed to have warblers on Aride and Cousine, respectively, and to John Neville for assistance on Cousin Island from September 1990 to June 1991. We thank the staff on the Islands of Cousin and Cousine for helping with practicalities of the project (transport and shopping). We thank especially Robbie Bresson, Alain Bresson, James Bresson, John Soyana, Raymond Laramie from Cousin, and George and Juliane Souffe from Cousine. Helpful criticisms of an early draft of the manuscript were provided by Nick Davies, Tony Fox and two anonymous referees.

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